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STUDIES ON EAST AFRICAN ACRIDOIDEA (ORTHOPTERA), WITH SPECIAL REFERENCE TO EGG-PRODUCTION, HABITATS AND SEASONAL CYCLES

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With 1 Text-figure

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I. Introduction

The observations on which the following account is based were made during 1950–1955 in Tanganyika Territory, as a spare-time occupation. During 1950 an attempt was made to dissect 20 females of each of as many species as could be found and to record data on the ovaries. From 1951 onwards this work was continued as species new to the author were encountered, but the main work was the collection and dissection of 20 females per month of selected species throughout the year. In selecting species, the only factors considered were availability in the area and number of ovarioles. Species which normally have more than 20 ovarioles per ovary were not regularly dissected because of the limited time available.

II. Geographical Areas

For the monthly dissections throughout a year, specimens were taken as far as possible from the same areas each week, in the hope that substantially the same population would thus be sampled. This was not always possible,

on account of movements in the course of the author's employment. In 1950 and from 1st August to 18th September, 1951 grasshoppers were caught mainly at the Malaria Laboratory Field Station, Muheza, near Tanga. From 19th September to 31st October, 1951 they were caught on Kibaranga Sisal Estate, about 12 miles from Muheza (referred to as Kibaranga); during November again at Muheza, near the Railway Station, and from December 1951 to August, 1953 at the Sisal Research Station, Mlingano, between Muheza and Kibaranga (referred to as Mlingano). All these areas together are referred to for convenience as the Tanga area.

From September, 1953 to February, 1955 the author was stationed in Morogoro. Specimens were taken at various places between Ruvu and Kilosa, and the localities are described in more detail where necessary below. The whole area is referred to as the Central Line area. In addition, grasshoppers were caught in other parts of Tanganyika while the author was on longer journeys.

Meteorological records are quoted in connection with seasonal occurrence of grasshoppers. These are from Mlingano and rainfall records cannot be rigidly applied to Muheza and Kibaranga because of the great local variation. It is apparent that the Tanga area receives a well-distributed rainfall, no month throughout the two years being entirely rainless. The " long rains " usually occur approximately from April to July and the " short rains " from October to December, though there is much variation from year to year in amount and duration. Herbaceous plants and grass grow throughout a normal year and there is never any shortage of food nor of suitable cover for grasshoppers. The soil is red laterite which forms a very hard surface during dry weather and into which light rain scarcely penetrates. During long dry spells the soil may crack where it is bare, but this is not common on a large scale.

In most of the Central Line area rainfall is also well distributed, though amounts are less than in the Tanga area, especially in amount of rain falling in the wet seasons. These comprise the months March–May and October–November. Annual totals on a sisal estate near Morogoro have varied from 18 to 54 inches since 1945. It was not possible to collect figures for rainfall in this area while work was going on there, though, as no regular dissections were made, this is not important. Plant growth during the dry seasons is slow and there is more bare soil to be seen than in the Tanga area.

III. Material and Methods

Grasshoppers were caught with a net by walking through an area where the species sought was expected to occur. Catches were random to the extent that an individual once put up was followed until caught or lost. However, winged East African grasshoppers tend to make prolonged flights. On first disturbance they usually fly for a short distance, up to 20 yards. On the second, the distance is increased and those which live amongst thick herbage may creep inside, where they are seldom found. It is often possible to follow up for a long time those species which live amongst short grass. An account of the evasive behaviour of some species is given below (pp.42–49).

The grasshoppers were dissected under a binocular microscope, usually within a few hours. The particulars recorded are detailed in the following paragraphs.

The number of ovarioles in each ovary was counted, and the number of these which were " small ", *i.e.* in which egg 1 was much smaller than in the others.

The total number of egg rudiments in five ovarioles chosen at random was counted.

The stages used to classify egg-development were those used by the author in earlier work on *Locusta migratoria migratorioides* (Phipps, 1950) and on British grasshoppers (Phipps, 1949). They are as follows :

Stage I.—Ovaries immature, the lowest egg in each ovariole (egg 1) yolkless. No evidence that oviposition has ever occurred.

Stage II.—Egg 1 coloured faintly yellow by deposition of yolk.

Stage III.—Egg 1 definitely containing yolk, larger than in stage II.

Stage IV.—Grasshoppers in which ovulation has occurred at least once. This stage therefore includes all those with eggs in the oviducts and all those in which the presence of *corpora lutea* shows that ovulation has occurred, though the eggs may no longer be found in the oviduct.

The length of egg 1 was measured with an eyepiece micrometer and in some cases also the length of the next egg above it (egg 2).

When eggs were present in the oviducts, the number in each oviduct was counted and the length of a few of the eggs was measured and the mean recorded as the egg-length ; there was seldom much variation in size between the eggs in one specimen.

It was noted that when grasshoppers were killed in chloroform vapour the ovipositor valves sometimes gaped widely and sometimes remained pressed together. This condition was recorded as " open " or " closed ". It seems that the valves open if the apodemes have hardened sufficiently and this may be a useful method of determining whether a grasshopper is under or over a certain age.

The presence of parasites or of abnormalities was recorded, and also whether the grasshopper was taken *in copula.*

The specimens were finally dried, papered, given a serial number and sent to Dr. V. M. Dirsh at the Anti-Locust Research Centre or to Mr. D. K. McE. Kevan at the University of Nottingham for determination. Later, some of each species were measured, using a calliper gauge and taking the length from the tip of the head to the point where the dorsal and ventral ovipositor valves meet, otherwise an error of 1 mm. may be introduced between those in which the valves are open and those in which they are closed.

Most of the specimens are in the collections of the British Museum (Natural History) ; the rest are in the possession of Prof. D. K. McE. Kevan at McGill University.

The species dissected throughout a complete year were : *Chrotogonus hemipterus* Schaum, *Paraspathosternum pedestre* (Miller), *Parepistaurus* sp. n.,[1] *Catantops melanostictus* Schaum, *Phaeocatantops decoratus* (Gerstaecker), *Oxyaeida poultoni* Ramme, *Aiolopus* sp. aff. *A. thalassinus* (Fab.), subsequently referred to as *Aiolopus* sp., *Morphacris fasciata* (Thunberg), *Trilophidia conturbata* (Walker), *Acrotylus patruelis* (Herrich-Schaeffer) and *Gymnobothrus temporalis flexuosus* (Schult.).

[1] This species is to be described elsewhere by Prof. D. K .McE. Kevan.

Johnston (1956) has been followed for taxonomy and nomenclature, but the major group classification is that proposed by Dirsh (1956).

IV. Results of Dissection

(1) *Anatomy*

The anatomy of the female reproductive system of Acrididae has recently been described by Waloff (1954) and by the author (Phipps, 1949 and 1950). A short note on the structure of the ovaries of Eumastacidae has appeared elsewhere (Phipps, 1958). They do not differ fundamentally from those of Acrididae.

(2) *The Numbers of Ovarioles*

The results of the present investigation are set out in Table I, without regard to seasonal variations. As Waloff (1954) has pointed out, the variation in the number of ovarioles within a species increases with the rise in their numbers. Very few of the species now under consideration had fewer than 10 ovarioles in each ovary, and often where only 20 specimens were dissected no two had the same combination of numbers of ovarioles in the two ovaries. For this reason, average numbers of ovarioles are given.

Table I.—*Numbers dissected, where and when caught, average length of female in mm., average ovarioles per female, average ovarioles per mm. length of female, percentage "small" ovarioles and average number of eggs in oviducts (no. of females in brackets) for all species of Acridoidea studied*

Species	Number	Place and date	Length in mm.	Av. ovar.	Ovar. per mm.	% small	Av. eggs
Family Lentulidae							
Rehnula usambarica (Ramme)	11	Mlingano, iv.52–i.53	15·4	8·0	0·5	.	8 (1)
Rehnula sp.	1	Korogwe, xi.52	15·4	8	0·5	.	.
Usambilla modicicrus (Karsch)	1	Soni, ix.50	18·0	8	0·4	.	.
U. olivacea Sjöstedt	1	Korogwe, viii.52	15·4	8	0·5	.	.
Usambilla sp.	1	Morogoro, viii.54	.	8	.	.	.
Mecostibus minor	1	Mlingano	21.0	.	.	.	17 (1)
Family Acrididae							
Subfamily Hemiacridinae							
Oriastes luridus Karsch	1	Magrotto	50·0	60	1·2	26·7	.
	7	Mlingano, iii.52–i.53	43·0	52·0	1.2	4·7	.
	4	Morogoro, ii.55	40·0	54·3	1·6	26·2	41 (1)
Meruana usambarica Karsch	12	Mlingano, iii.52–vii.53	37·6	26·0	0·7	17·3	22·3 (4)
Paraspathosternum pedestre (Miller)	10	Muheza, viii.50	22·3	18·1	0·8	2·8	.
	133	Mlingano	21·6	18·6	0·9	7·8	15·9 (12)
Kassongia sp.	3	.	20·5	13·7	0·7	2·4	.

TABLE I—*cont.*

Species	Number	Place and date	Length in mm.	Av. ovar.	Ovar. per mm.	% small	Av. eggs
Subfamily CATANTOPINAE							
Afroxyrrhepes brevifurca Uvarov	6	Morogoro, xi.53–ii.55	55·4	86·8	1·8	5·2	.
Tristria sp.	1	Pangani, iii.52	30.0	18	0·6	22·2	.
Oxya hyla Serv.	10	Muheza, viii.50	27.0	23·1	0·9	7·0	20 (1)
Eucoptacra exigua	10	„ „	18·9	8·8	0·5	.	8·5 (2)
I. Bol.	6	Mlingano, 1951	.	8·8	.	7·6	7·7 (3)
	4	Morogoro, 1955	15·0	7·9	0·5	.	.
Parepistaurus sp. n.	186	Mlingano	15·3	8·0	0·5	10·5	6·7 (25)
P. lobicercus Uvarov	15	Morogoro, vi.54–iii.55	15·3	8·0	0·5	6·7	7·3 (3)
Abisares viridipennis azureus Sjöstedt	16	Mlingano, iv.52–i.53	38·0	58·0	1·5	2·4	51·3 (4)
Aresceutica subnuda	1	Kwamtili	20·0	19	0·7	.	19 (1)
Karsch	5	Ulugurus	23·5	23·6	1·0	3·4	24 (1)
Pseudophialosphera tectifera (Ramme)	13	Mlingano	25·8	22·3	0·9	1·0	24 (1)
Ixalidium assymetricum	10	Soni	30·0	15·6	0·5	.	12 (1)
(Ramme)	9	Mlingano	26·6	11·4	0·4	2·0	12·5 (2)
Ischnansis burtti	11	Mlingano	26·7	29·3	1·1	0·9	.
Uvarov							
Eupropacris ornata	9	Mlingano	30·0	42·6	1·4	0·3	.
Karny							
Pseudopropacris vana	3	„	33·5	49·7	1·5	2·0	.
(Karsch)							
Catantops axillaris	12	Pangani	35·4	71·3	2·0	12·3	67·5 (2)
axillaris (Thunberg)							
C. melanostictus	20	Muheza, viii.50	24·1	31·7	1·3	9·3	27·0 (2)
Schaum	170	Mlingano	25·9	29·1	1·1	8·0	27·6 (26)
	7	Morogoro	.	33·4	.	4·2	34 (1)
C. spissus adustus	1	Nachingwea	.	49	.	.	.
(Walker)							
Phaeocatantops decoratus	10	Muheza, viii.50	29·0	34·6	1·2	4·4	36·5 (2)
(Gerst.)	224	Mlingano	25·5	34·6	1·4	8·8	28·9 (25)
	4	Morogoro	24·0	35·6	1·5	5·6	.
Anacatantops notatus	1	Muheza	20.6	33	1·6	21·2	.
(Karsch)							
Cardenius pauperatus	5	Morogoro	28·4	31·2	1·1	21·2	.
(Karny)							
Stenocrobylus cervinus	7	Mlingano	26·7	19·7	0·8	2·9	.
Gerst.	1	Morogoro	.	25	.	.	.
Schistocerca gregaria	6	Handeni, ii.54	.	85.8	.	.	.
(Forsk.)							
Anacridium wernerellum	4	Mlingano	52·0	169·2	3·3	0·9	151 (1)
(Karny)							
Ornithacris sp.	3	„	63·0	146·0	2·3	.	154 (1)
	3	Morogoro	63·0	146·0	2·3	11·2	.
Cyrtacanthacris tatarica	10	Muheza	60·5	199·2	3·3	6·3	187·5 (2)
(L.)							
Kraussaria dius	7	Mlingano	48·4	80·3	1·7	.	.
(Karsch)							
Eyprepocnemis plorans	10	Muheza	34·3	74·6	2·2	7·4	51·0 (2)
(Charpentier)							

TABLE I—*cont.*

Species	Number	Place and date	Length in mm.	Av. ovar.	Ovar per mm.	% small	Av. eggs
Subfamily CANTANOPINAE—*cont.*							
Oxyaeida poultoni	10	Muheza	27·7	34·2	1·2	5·3	.
Ramme	159	Mlingano	28·2	34·4	1·2	12·4	24·6 (15)
Thisoicetrus coerulescens	7	Mlingano, viii.50	46·2	152·7	3·5	.	82 (1)
(Stål.)	2	Mombasa, ix.50	.	129·0	.	.	.
	9	Morogoro	34·3	122·1	3·5	9·7	.
T. coerulipes (Sjöstedt)	8	Mlingano	44·0	67·5	1·5	3·3	.
T. pulchripes (Schaum)	1	,,	44	67	1·4	.	.
Taramassus cunctator	10	Muheza	25·0	45·2	1·8	17·7	28 (1)
(Karsch)							
Cataloipus oberthuri	9	,,	56·0	121·9	2·2	11·2	.
I. Bol.	5	Morogoro	52·3	109·0	1·9	7·0	98·5 (2)
Tropidiopsis pendulus	10	Muheza	38·2	49·8	1·3	.	.
(Karsch)							
Tylotropidius speciosus	1	Morogoro	.	70	.	10·0	.
(Walker)							
Subfamily ACRIDINAE							
Aiolopus sp.	22	Muheza	23·3	29·9	1·3	6·7	27·7
Aiolopus sp.	202	Mlingano	23·9	30·8	1·3	10·0	25·0 (41)
	10	Morogoro	23·0	32·1	1·4	6·2	30·0 (6)
A. longicornis Sjöstedt	10	Muheza	28·5	37·4	1·3	9·9	30·5 (2)
	11	Mkata	28·0	37·6	1·3	22·8	34·0 (3)
Jasomenia sp.	11	Muheza	24·3	37·8	1·6	12·7	38·5 (2)
Morphacris fasciata	20	,,	27·9	34·5	1·2	9·5	29·0 (5)
(Thun.)	178	Mlingano	26·9	35·2	1·3	13·0	28·0 (28)
Trilophidia conturbata	20	Muheza	17·0	20·8	1·2	15·1	12 (1)
(Walker)	209	Mlingano	18·0	23·6	1·3	11·7	17·1 (35)
Acrotylus apricarius	4	Mkata	18·0	13·0	0·7	3·8	10 (1)
Stål							
A. elgonensis Sjöstedt	1	Ruvu	.	11	.	.	9 (1)
A. furcifer aurantius	7	Soni	16·5	11·6	0·7	22·2	9 (1)
Uvarov							
Acrotylus patruelis	20	Muheza	25·9	22·8	0·7	10·7	16·7 (3)
(Herrich-Schaeffer)	87	Mlingano	21·9	23·1	1·0	11·7	16·9 (13)
	7	Morogoro	25·9	24·6	1·0	10·5	.
A. variegatus Brancsik	10	,,	19·9	21·1	1·1	5·2	18 (1)
Acrotylus sp.	25	,,	24·6	20·1	0·8	5·6	17·7 (6)
Acrotylus sp.	2	,,	20·5	16·5	0·8	.	13 (1)
Oedaleus citrinus	2	Mlingano	29·0	35·0	1·2	16·7	.
Saussure	4	Morogoro	29·0	36·8	1·3	5·7	38 (1)
O. senegalensis (Krauss)	2	Mlingano	26·0	36·5	1·4	.	29 (1)
Humbe tenuicornis	20	Muheza	31·9	47·8	1·5	9·3	41·5 (4)
(Schaum)	6	Morogoro	.	49·0	.	14·6	.
Gastrimargus africanus	1	Morogoro	48	119	2·5	.	.
(Saussure)	10	Muheza	41·5	72·4	1·8	7·2	.
Gastrimargus sp.	1	Usambaras	.	115	.	.	.
Heteropternis saussurei	6	Muheza	24·8	22·2	0·9	0·8	22·0 (2)
Kirby	4	Magrotto	24·8	22·0	0·9	6·8	.
H. thoracica (Walker)	1	Muheza	.	21	.	.	.
Paracinema tricolor	10	Muheza	38·4	159·3	4·1	12·1	116 (1)
(Thunberg)	3	Morogoro	.	130·5	3·4	17·7	.
Gymnobothrus fallax	2	Ulugurus	22·0	23·5	1·1	27·8	.
elongatus (Miller)							
G. fallax fallax (Karny)	1	Morogoro	.	17	.	3·6	.
G. linea-alba I. Bol.	1	Ulugurus	.	10	.	.	10 (1)

TABLE I—*cont.*

Species	Number	Place and date	Length in mm.	Av. ovar.	Ovar. per mm.	% small	Av. eggs
Subfamily ACRIDINAE—*cont.*							
G. temporalis	20	Muheza	21·2	16·0	0·8	14·1	15·0 (3)
flexuosus (Schult.)	208	Mlingano	19·7	16·3	0·8	14·8	12·7 (28)
	18	Morogoro	20·4	16·2	0·8	11·7	16·7 (6)
	1	Pangani	22·0	21	1·0	.	18 (1)
Gymnobothrus sp.	1	Muheza	21·5	20	0·9	.	.
Gymnobothrus sp.	10	Usambaras	19·6	14·3	0·7	4·9	.
Gymnobothrus sp.	1	Morogoro	.	18	.	5·5	.
Gymnobothroides pullus Karny	11	Ulugurus	16.4	14·3	0·9	3·8	13·5 (2)
Gymnobothroides sp.	10	Soni	19·0	13·8	0·7	3·6	12·5 (2)
Comacris semicarinatus (Gerstaecker)	11	Tanga	22·3	11·7	0·5	16·3	11 (1)
Duronia liturata (I. Bol.)	12	Morogoro	35·8	54·1	1·5	1·0	53·0 (5)
D. tricolor (Karny)	2	,,	30·0	48·5	1·6	13·4	29 (1)
Orthochtha sp.	10	Muheza	35·8	30·9	0·9	1·3	28 (1)
Machaeridia sp.	10	,,	29·2	16·9	0·6	3·0	18 (1)
Odontomelus brachypterus	2	Usambaras	24·0	16·5	0·7	.	.
(Gerst.)	9	Morogoro	21·5	16·2	0·8	2·0	.
Odontomelus sp.	2	Tanga	20·5	10·5	0·5	.	.
Odontomelus sp.	1	Korogwe	23·0	16	0·7	43·7	.
Odontomelus sp.	2	Mkata	18·0	14·5	0·8	34·6	12·5 (2)
Acrida sulphuripennis	10	Muheza	55·1	89·4	1·6	3·5	88 (1)
(Gerst.)	1	Morogoro	50·5	79	1·6	3·8	.
Subfamily TRUXALINAE							
Pnorisa squalis Stål	3	Korogwe	23·5	26·7	1·1	7·5	25 (1)
	13	Mkata	24·6	27·0	1·1	5·7	23·8 (4)
Pseudogmothela sp.	1	,,	20·0	13	0·7	.	13 (1)
Afrohippus brevipennis (Miller)	5	,,	18·0	14·6	0·8	24·6	12·5 (2)
Platypternodes sp.	4	,,	28·5	38·5	1·4	8·5	.
Brachycrotaphus sjostedti Uvarov	2	Morogoro	31·0	14·5	0·5	10·3	11 (1)
Mesopsis laticornis (Krauss)	5	,,	62·0	33·0	0·5	2·4	36 (1)
Truxalis conspurcata somalia (Burr)	5	,,	58·0	82·4	1·4	5·3	78 (1)
Truxaloides braziliensis (Drury)	1	,,	57·5	88	1·6	.	.
Subfamily CALLIPTAMINAE							
Caloptenopsis ferrifer (Walker)	2	Ulugurus	29·0	41·5	1·4	4·8	40·0 (2)
C. glaucopsis meruensis (Sjös.)	21	Morogoro	30·2	50·5	1·7	8·3	53·5 (2)
C. speciosa Sjöstedt	3	Mlingano	32·7	50·3	1·6	.	.
	2	Morogoro	36·0	60·0	1·7	25·0	.
Acorypha pallidicornis (Stål)	1	Kondoa Irangi	.	41	.	.	.
FAMILY PYRGOMORPHIDAE							
Chrotogonus hemipterus	20	Muheza, viii.50	18·0	27·2	1·5	18·0	19·3 (4)
Schaum	237	Mlingano	17·1	27·7	1·6	11·6	21·0 (77)
	76	Morogoro	.	29·6	.	14·5	22·2 (29)

TABLE I—*cont.*

Species	Number	Place and date	Length in mm.	Av. ovar.	Ovar. per mm.	% small	Av. eggs
FAMILY PYRGOMORPHIDAE—*cont.*							
Dictyophorus grisea (R. and F.)	1	Ruvu	50·1	69	1·4	.	.
Maura modesta I. Bol.	1	Morogoro	36·0	43	1·2	.	.
Taphronota calliparea	10	Soni, ix.50	41·4	99·4	2·4	11·5	.
(Schaum)	3	Ulugurus	39·7	96·0	2·4	11·5	.
Phyteumas olivaceus (Karsch)	9	Morogoro	72·4	297·0	4·1	5·2	.
Phymateus viridipes	1	Usambaras	.	212	.	.	.
Stål	1	Morogoro	53·5	161	3·0	3·7	.
Zonocerus elegans	6	Korogwe	44·0	126·0	2·9	0·5	121 (1)
(Thunberg)	21	Morogoro	44·0	127·0	2·9	26·0	.
Atractomorpha gerstaeckeri I. Bol.	10	Muheza, viii.50	28·8	67·3	2·3	2·8	56 (1)
FAMILY PAMPHAGIDAE							
Lamarckiana sp.	14	Morogoro	60·2	80·3	1·3	5·0	76·0 (2)
FAMILY EUMASTACIDAE							
Plagiotriptus hippiscus (Gerst.)	9	Mlingano and Morogoro	18·0	67·9	3·8	12·4	85 (1)
Clerithes sp.	1	Morogoro	12·0	16	1·3	.	13 (1)
Thericles gnu Karsch	7	Mlingano	13·6	17·1	1·3	1·7	13·5 (2)
Euschmidtia sp.	2	„	.	32·5	1·2	.	.
Euschmidtia sp.	3	Mlingano and Morogoro	28·0	29·0	1·0	6·9	.
Euschmidtia sp.	1	Morogoro	.	26	0·9	.	26 (1)
FAMILY TETTIGIDAE							
Paratettix scaber group	2	.	.	22·0	.	9·1	.

Regressions of ovariole number on female length were calculated as was done by Waloff (1954). It should be noted, in comparing her results with mine, that she based her calculations on the average number of ovarioles in one ovary, whereas mine are based on the total ovarioles in the two ovaries. It should also be mentioned that where at least five specimens of the same species were taken in each of two widely separated areas, they have been treated as distinct species in these calculations. Species for which no female length is given in Table I are, of course, omitted. The equations are as follows, where y = no. of ovarioles and x = length of female in millimetres. The value of P gives the significance of the regression coefficient.

Family ACRIDIDAE

Sub-family Catantopinae

Group Catantopes $y = 37{\cdot}0 + 2{\cdot}55\ (x - 27{\cdot}7)$ $P < 0{\cdot}05$ 8 spp.

Group Eyprepocnemes $y = 83{\cdot}76 + 2{\cdot}47\ (x - 40{\cdot}25)$ $P < 0{\cdot}05$ 10 spp.

Groups Cyrtacanthacres and Dericorythi, not significant, each 4 spp.

Groups Oxyae, Coptacrae, Oxyrrephes (1 sp. each), Lepismae (2 spp.), not tested.

Whole subfamily $y = 68{\cdot}35 + 3{\cdot}38\ (x - 35{\cdot}5)$ $P < 0{\cdot}001$ 31 spp.

Sub-family Acridinae

Group Oedipodae $y = 35{\cdot}4 + 1{\cdot}9724\ (x - 24{\cdot}3)$	$P < 0{\cdot}01$	24 spp.
Group Acridae $y = 37{\cdot}7 + 1{\cdot}507\ (x - 30{\cdot}7)$	$P < 0{\cdot}05$	12 spp.
Group Pargi not significant		11 spp.
Whole sub-family $y = 31{\cdot}6 + 1{\cdot}719\ (x - 25{\cdot}2)$	$P < 0{\cdot}001$	47 spp.

Sub-family Hemiacridinae

$y = 34{\cdot}7 + 1{\cdot}544\ (x - 33{\cdot}6)$	$P < 0{\cdot}05$	7 spp.

The regressions for the sub-families Truxalinae (7 spp.) and Calliptaminae (4 spp.) were not significant.

Family Pyrgomorphidae

$y = 102{\cdot}3 + 4{\cdot}5743\ (x - 41{\cdot}17)$	$P < 0{\cdot}01$	8 spp.

No relation between ovariole number and female length was found for 6 species of Eumastacidae.

In some of these groups the lack of significance in the value of b appears to be due to the small number of species, but this may not be the case in, for example, the Group Pargi. The value of b for the Catantopinae exceeds that for the Oedipodae and so agrees with Waloff's results (1954). There are no significant differences among the slopes for any of the sub-divisions of the Acrididae, but that for the Pyrgomorphidae is significantly greater than those for all the Acridid sub-families. The large value of 4·5743 is due to high numbers in two genera only.

The number of ovarioles per millimetre of female length was also calculated for each species. The results are included in Table I, and are summarised for families and sub-families in Table II. As Waloff (1954) found, most species of Acridinae have rather few, less than one ovariole in all to each millimetre. A considerable number of Catantopinae have no more, and only the Pyrgomorphidae and Calliptaminae have at least one ovariole per millimetre.

Table II.—*Number of ovarioles per* 1 *mm. length of female.*

Number of spp. of	0·40–0·99	1·0–1·59	1·6–2·19	2·2–3·79	2·8–2·39	3·4–3·99	Over 3·99
Acrididae							
Catantopinae .	9	12	6	3	2	1	0
Acridinae .	18	12	4	1	0	1	1
Truxalinae .	4	3	1	0	0	0	0
Hemiacridinae .	3	1	1	0	0	0	0
Calliptaminae .	0	1	2	0	0	0	0
Pyrgomorphidae	0	3	1	2	2	0	1
Lentulidae .	4	0	0	0	0	0	0
Eumastacidae .	1	4	0	0	0	1	0

Differences between the two ovaries in the number of ovarioles they contained were also considered. Information on asymmetry in all the species which were dissected throughout a year and in some other species of which fewer were dissected but which are interesting because of the high or low ovariole number, is summarised in Table III. It appears that asymmetries greater than 4 occur in a considerable proportion of individuals only in those species with more than

50 ovarioles, asymmetries up to 4 only in those with more than 30 ovarioles, up to 3 only in those with more than 20 and up to 2 only in those with more than 12. *Parepistaurus* particularly departs very seldom from 4 ovarioles in each ovary, while *Eucoptacra*, in which 4 and 4 is quite usual, departs much more frequently from it. In all other species dissected, except *G. temporalis*, at least half were asymmetrical. Only in *Lamarckiana* sp. and *Atractomorpha gerstaeckeri* were no symmetrical examples found.

TABLE III.—*Asymmetry in respect of numbers of ovarioles in the two ovaries in selected species*

Species	Percentage of females with asymmetry of						Average ovarioles	Number dissected
	0	1	2	3	4	>4		
P. olivaceus	11·0	0	0	0	0	89·0	297·0	9
P. tricolor	40·0	0	10·0	20·0	10·0	20·0	159·3	10
C. oberthuri	14·3	21·4	7·0	35·7	0	21·6	121·9	14
Lamarckiana sp.	0	28·6	28·6	0	14·2	28·6	80·3	14
G. africanus	20·0	40·0	10·0	20·0	10·0	0	71·8	10
A. gerstaeckeri	0	30·0	30·0	30·0	10·0	0	67·3	10
C. speciosa	9·0	28·0	24·0	19·5	0	19·5	50·5	21
H. tenuicornis	10·6	36·8	42·0	10·6	0	0	47·1	19
M. fasciata	27·2	44·0	17·8	8·9	2·1	0	35·2	180
P. decoratus	23·1	53·0	18·7	4·9	0·3	0	34·6	225
O. poultoni	27·1	40·9	21·4	7·5	2·4	0·6	34·4	159
Aiolopus sp.	28·7	44·0	19·4	5·5	2·4	0	30·8	202
C. hemipterus (Morogoro)	24·0	44·0	24·0	8·0	0	0	29·6	75
C. melanostictus	29·6	46·3	16·1	6·2	1·2	0·6	29·1	162
C. hemipterus (Mlingano)	30·8	45·5	19·5	3·0	0·4	0·8	27·7	237
T. conturbata	42·5	42·9	12·8	0·9	0·9	0	23·6	214
A. patruelis	37·5	52·3	8·0	2·2	0	0	23·1	88
P. tectifera	54·0	38·4	7·6	0	0	0	22·3	13
Acrotylus sp.	24·0	52·0	20·0	4·0	0	0	20·1	25
G. temporalis	58·2	37·5	4·3	0	0	0	19·7	208
P. pedestre	49·0	46·0	4·5	0·5	0	0	17·8	133
Gymnobothroides sp.	50·0	40·0	10·0	0	0	0	13·8	10
I. asymmetricum	45·0	55·0	0	0	0	0	11·4	9
E. exigua	60·0	40·0	0	0	0	0	8·7	20
Parepistaurus sp. n.	97·5	2·5	0	0	0	0	8·0	186

Comparison of asymmetry in stages I and IV for species dissected through the year shows no increase in the proportion asymmetrical in stage IV, though there are examples of higher asymmetry which do not occur in stage I. This may be due only to the larger numbers of stage IV dissected. The possible significance of asymmetry is discussed below (p. 42).

(3) *The Eggs and their Development*

Numbers and Sizes of Eggs

Mean numbers of eggs in the oviducts for each species are included in Table I. In addition, specimens of a few species were kept in cages and the pods examined, all at Mlingano. Numbers of eggs were, for *Catantops melanostictus*, mean 28·7, range 25–30, 7 pods; for *Gymnobothrus temporalis flexuosus*, mean 13·5,

range 12–26, 18 pods ; for *Aiolopus* sp. 16, 1 pod. The numbers of eggs per pod for the first two are higher than the mean numbers found in the oviduct, and it may be that some of those with eggs in the oviducts were caught whilst ovipositing.

Stages I–IV have been defined in Section III. Limiting sizes of eggs in these stages for each species are set out in Table IV. This includes only those species in which information is available for egg-size in more than one stage. The smallest size quoted for egg 1 is not necessarily its size immediately after final ecdysis, as in some species no newly-emerged females were dissected, but in those which were dissected throughout a year the minimum size is in every case 0·31 mm. and it seems very probable that the initial size of egg 1 is fairly constant and bears little relation to the size of the grasshopper. This point is further elaborated below. In most species few or no examples in stage II were dissected. The length of egg 1 in this stage may be taken as that at which the deposition of yolk begins. There is clearly considerable variation within many species, but in most the lower limiting size in stage II agrees fairly well with the upper limit in stage I. The size of egg 1 when yolk deposition begins also appears to bear little relation to the size of the grasshopper.

The size of egg 1 in stage IV with eggs in the oviducts shows considerable spread in most species. The lower limit is usually within or below the range for stage II, the upper limit often within the range for Stage III, though never reaching the minimum size for an egg from the oviduct. This suggests that there is considerable variation within a species either in the time elapsing between ovulation and oviposition, during which growth of egg 1 occurs, or in the size of egg 2 at ovulation (which then becomes egg 1). The fact that the minimum size of egg 1 in stage IV without eggs in the oviduct is in many species no greater than its minimum in those with eggs in the oviduct shows that oviposition may occur very shortly after ovulation. There is always some growth of egg 1 between oviposition and the next ovulation, as the maximum size of egg 1 in stage IV without eggs in the oviducts is always greater than its maximum size in those with eggs in the oviducts.

The length of the empty follicle was measured in most grasshoppers with eggs in the oviducts, and also in those without eggs but in which the follicle was larger than usual, indicating recent ovulation and oviposition. The occurrence of such specimens also indicates that oviposition may occur very soon after ovulation, but in most species almost half of those with eggs in the oviducts had considerably shrunken follicles, showing that oviposition may be delayed. A notable exception to this is *Paraspathosternum pedestre*, in which 11 out of 13 with eggs in the oviducts had large follicles, and which appears therefore to oviposit soon after ovulation.

It was hoped that an estimate of the rate of shrinkage of the follicle in terms of growth of egg 1 might be made. However, there is no correlation between follicle size and size of egg 1 for any species.

Regressions of mean egg length on female length were calculated for Catantopinae (24 spp.), Acridae (10 spp.) and Oedipodae (15 spp.) The equations were as follows :

Catantopinae	$y = 5{\cdot}09 + 0{\cdot}055481\ (x - 29{\cdot}81)$	$P < 0{\cdot}001$
Acridae	$y = 4{\cdot}597 + 0{\cdot}073182\ (x - 27{\cdot}24)$	$P < 0{\cdot}001$
Oedipodae	$y = 4{\cdot}18 + 0{\cdot}18413\ (x - 23{\cdot}47)$	$P < 0{\cdot}01$

This means that for each increase of 1 mm. in female length, the length of the egg increases on the average by 0·055481 mm. in Catantopinae, by 0·073182 mm. in Acridae and by 0·18413 mm. in Oedipodae. The slope is significantly greater for the Oedipodae than for the other two groups, but there is no significant difference between the slopes for Catantopinae and Acridae. The values of mean female length are not the same in these equations as in those for regression of ovariole number on female length because some species do not appear in the second set of equations, as no individuals with eggs in the oviducts were dissected. This includes many of the larger Catantopinae, which makes the mean in the egg length/female length equation much smaller than in the ovariole number/female length equation for this sub-family.

TABLE IV.—*Limiting sizes of egg* 1 *in mm. in different stages. "With eggs" and "Without eggs" refers to eggs in the oviduct*

	Stages					
	I	II	III	IV with eggs	IV without eggs	egg
R. usambarica	0·63	.	3·88	1·25–1·88	2·19–2·81	3·75
O. luridus	0·63–0·94	.	.	1·80	1·80–5·50	5·49
M. usambarica	.	.	2·94–5·00	1·25–3·13	3·13–5·00	5·00–5·31
P. pedestre	0·31–1·25	0·94–1·69	1·56–5·00	1·25–2·50	1·25–4·75	4·05–5·40
E. exigua (Mlingano)	.	.	.	2·19–3·13	3·13–4·50	3·75–4·38
E. exigua (Morogoro)	.	.	.	.	1·80–3·60	4·06–4·38
Parepistaurus sp. n.	0·31–1·25	1·25–2·19	1·25–4·06	1·25–3·12	2·19–5·00	3·88–5·00
P. lobicercus	0·45–0·90	.	4·05–4·23	1·80–2·25	3·60–4·59	4·05–4·25
A. viridipennis	0·63–0·94	.	.	1·25–1·88	1·56–6·25	6·88–8·13
A. subnuda	0·63–0·94	.	2·50	2·19	3·44	6·13
P. tectifera	0·63	.	1·56	1·56–1·88	1·56–6·25	4·38–5·00
I. asymmetricum	0·31	.	.	1·88–2·81	3·13–5·00	4·69
I. burtti	0·94	1·56–2·19	1·56–3·25	3·13	1·25–5·00	.
E. ornata	0·31–0·63	1·26	.	.	2·19	.
P. vana	.	1·25	5·81	.	5·00	.
C. axillaris	.	.	.	2·19	3·13	4·69
C. melanostictus (Mlingano)	0·31–1·38	1·38–2·50	1·88–5·31	1·25–3·13	1·25–5·00	4·06–5·31
C. melanostictus (Morogoro)	0·45	.	4·32	2·34	4·05–4·95	4·05
P. decoratus	0·31–1·25	1·06–2·01	1·88–5·31	1·06–3·13	1·25–5·31	4·69–5·63
C. pauperatus	0·45	.	5·94	.	2·25–5·85	.
S. cervinus	.	0·94–1·56	1·88–3·13	.	2·50–3·75	.
A. vernerellum	.	.	2·50–3·13	2·50	1·88	6·25
Ornithacris sp.	0·63–0·94	1·56–2·19	.	2·19	6·88	6·25
K. dius	0·63–0·94	1·25	1·56	.	2·94	.
O. poultoni	0·31–1·38	0·94–1·25	1·25–5·00	0·94–1·88	0·94–4·69	3·94–4·50
T. caerulipes	0·63	2·50–3·44	2·50–4·06	.	2·38–4·69	.
C. oberthuri	0·63–1·35	1·88	5·00–6·03	1·35–4·50	.	6·30–6·75
C. glaucopsis	0·31–0·63	1·56	2·44–3·13	2·19–3·13	1·88–4·69	5·00–5·94
C. speciosa	0·31–0·63	.	.	.	4·50	.
G. temporalis (Mlingano)	0·31–1·38	1·25–2·81	2·50–4·25	1·06–3·13	1·06–4·50	3·56–4·37
G. temporalis (Morogoro)	0·45–1·35	1·62	1·80	2·70–3·15	3·15–4·77	.
G. pullus	0·63	.	3·13	1·57–2·50	2·81–4·06	3·75

TABLE IV—*cont.*

	Stages					
	I	II	III	IV with eggs	IV without eggs	egg
D. liturata	.	.	2·43–4·77	0·90–2·25	2·25–4·95	4·90–5·40
O. brachypterus	0·90–1·35	1·00	.	.	3·15–4·05	4·30–4·50
P. squalus	0·45	1·25	3·60–4·05	0·90–2·70	2·70–4·50	3·78–4·95
T. conspurcata	0·63	2·25	.	.	.	.
Aiolopus sp. (Mlingano)	0·31–1·88	1·25–2·19	2·81–4·38	0·94–4·06	0·94–4·06	3·44–4·37
Aiolopus sp. (Morogoro)	0·45	.	.	2·07–3·60	2·70–4·23	.
A. longicornis	0·63	.	.	1·25–2·70	2·50–3·13	4·40–4·50
M. fasciata	0·31–1·25	1·56–2·19	2·19–5·00	0·94–3·13	1·25–5·31	4·37–5·44
T. conturbata (Mlingano)	0·31–1·56	0·94–2·06	1·88–3·13	0·90–2·81	1·25–4·06	3·31–4·25
T. conturbata (Morogoro)	0·45–0·90	0·90	1·80–4·05	2·25	1·80–4·05	3·15
A. apricarius	.	.	3·15–3·60	2·70	5·40	4·50
A. patruelis	0·31–1·25	1·56	3·40–4·06	0·94–2·81	1·25–4·69	3·44–4·37
A. variegatus	0·45–1·35	1·35	3·15	2·70	2·70–4·32	4·05
Acrotylus sp.	0·94	.	.	1·56–3·13	1·00–5·00	4·68–5·58
Acrotylus sp.	0·45	.	5·13–5·22	1·80–5·04	1·80–5·13	4·68
O. citrinus	0·63–0·90	.	2·70–4·95	2·43	3·44–4·95	4·68
O. senegalensis	1·25	.	.	3·38	.	4·69
H. tenuicornis	1·80	1·80	2·70	.	4·05–5·40	.
P. tricolor	.	.	2·81	.	0·45–1·35	.
C. hemipterus (Mlingano)	0·31–1·25	0·94–2·06	1·88–3·13	0·90–2·81	1·25–4·06	4·06–5·00
C. hemipterus (Morogoro)	0·90	0·90–1·80	1·35–4·50	0·90–3·60	1·80–5·13	4·05–5·40
T. calliparea	.	.	2·19–5·31	.	6·25	.
P. olivaceus	0·90–3·60	.	6·66	.	2·70–7·65	.
Z. elegans	.	1·35–2·19	2·70–6·88	1·56	1·56–6·88	6·25
Lamarckiana sp.	0·90	.	3·15–8·10	3·24–5·85	4·50–7·65	8·10–8·50
P. hippiscus	0·45–0·94	1·25	1·88–4·38	2·25	1·88–4·38	4·86
Thericles sp.	0·63	.	3·25	0·94–2·19	1·88–3·44	3·44

It was noted that, though a tendency clearly exists for larger species to lay larger eggs, the length of the egg in small species is greater in relation to female length than in large. The smallest species for which information is available are *Parepistaurus* sp. n. and *P. lobicercus*, in both of which the average female length is 15·3 mm. The eggs are 4·34 and 4·18 mm. long respectively. The largest Catantopine dissected was *Ornithacris* sp., 60·3 mm. long and with a mean egg length of 6·25 mm. The largest eggs measured were those of *Lamarckiana* sp., 8·5 mm., the female being 60 mm. long. This suggests that there is a minimum size for a grasshopper egg and that the smaller number of ovarioles in the smaller species is forced on them by the need to maintain this minimum egg size. It was also observed that in small species, especially in *Parepistaurus*, when egg 1 is fully-developed, egg 2 is already yellow and may be more than half its size. This further suggests that in some small species reduction in the number of ovarioles has proceeded so far that enough food is

available to allow of more simultaneous growth of egg 1 and egg 2 than in the larger ones. This reduction may be connected with the accommodation of the eggs within the body cavity. If this surmise is true, the ratio

$$\frac{\text{length egg 1}}{\text{length egg in oviduct}}$$

might be greater for small species than for large ones.

Regression equations of this ratio on female length were calculated for Catantopinae, Acridae and Oedipodae separately and for all grasshoppers together without subdivision into taxonomic categories. It is significant only for all species together and the equation is

$$y = 0{\cdot}48 - 0{\cdot}0078926\ (x - 27{\cdot}35) \quad P \ll 0{\cdot}001$$

where $y = \frac{\text{egg 1}}{\text{egg from oviduct}}$ and $x =$ length of female in mm. Thus egg 2 grows more rapidly relative to egg 1 in small grasshoppers than in large ones. This also fits in with my comments on *Locusta migratoria migratorioides* (Phipps, 1950) that the ovarioles in females with eggs in the oviduct appear as small white appendages of the greatly swollen oviduct, and on British grasshoppers (Phipps, 1949) that any grasshopper which has already oviposited gives the impression, on being opened, of being almost ready to ovulate.

Duration and Recognition of Stages

The percentages of each stage taken in those species dissected through the year are shown in Table V. Singh (1958) finds that in *L. m. migratorioides* not all *corpora lutea* are pigmented ; in fact he describes ovarioles with pigmented *corpora lutea* as " sub-normal ". In the present observations the specimens assigned to stage IV were those with eggs in the oviducts and those with pigment spots in the pedicels of normal ovarioles. If " sub-normal " ovulation is not common it is therefore possible that some of the grasshoppers assigned to stage III were really in stage IV. The percentages of the stages may be taken as roughly proportional to their duration, if the effect of deaths, on which

TABLE V.—*Numbers of each stage, also expressed as a percentage of total females caught for certain species*

Species	Stage I		Stage II		Stage III		Stage IV	
	No.	%	No.	%	No.	%	No.	%
P. pedestre	21	15·9	14	10·6	26	19·7	71	53·8
Parepistaurus sp. n.	30	16·1	12	6·4	25	13·4	119	64·1
C. melanostictus	41	24·2	3	1·8	25	14·8	100	59·2
P. decoratus	54	24·2	7	3·1	34	15·3	128	57·4
O. poultoni	37	23·0	8	5·0	40	25·0	75	47·0
G. temporalis	29	13·9	2	1·0	28	13·4	149	71·7
Aiolopus sp.	74	37·6	3	1·5	28	14·2	92	46·7
M. fasciata	45	27·0	3	1·8	34	20·4	85	50·8
T. conturbata (Mlingano)	25	12·7	10	5·1	37	18·9	124	63·3
T. conturbata (Morogoro)	14	17·1	0	0	12	14·6	56	68·3
A. patruelis	18	20·6	2	2·3	17	19·5	50	57·6
C. hemipterus	45	19·7	12	5·2	47	20·6	125	54·5

no information is available, is neglected and it is assumed that no change in habitat occurs during maturation of the ovaries. These percentages are of the same order for most species and suggest that more than half the adult life is spent in stage IV and that stage III lasts as long as stage I. It seems unlikely that many of those placed in stage III were, in fact, in stage IV, as this would reduce the duration of stage III, in which considerable egg-growth occurs, to a small proportion of the total life. It is considered that " sub-normal " ovulation occurs often enough to make the presence of pigment spots in some ovariole pedicels a fairly reliable guide to the occurrence of ovulation, except where it is associated only with degenerating eggs.

" Small " Ovarioles

" Small " ovarioles are those in which egg 1 is very much less developed than in the others, and may be devoid of yolk. They are never recognisable in stage I, seldom in stage II and only become obvious in stages III and IV, by comparison with developed, yolk-laden eggs. They may be of two types, arising in different ways. If an egg 2 fails to grow, after ovulation, when it becomes egg 1, it will always be smaller than the others, though it may come to contain some yolk. It also happens not infrequently that egg 1 degenerates, and when this occurs it may have been as large as any of the others and have contained as much yolk. The yolk becomes darker than that of the other ovarioles, the egg shrinks and may become deformed. An intensely coloured *corpus luteum* is formed and, when degeneration is complete, the new egg 1, formerly egg 2, may be in the thread-like condition, only the presence of a very deeply coloured *corpus luteum* showing what has occurred. In these cases egg 2 is usually smaller than normal. Where small ovarioles were not separated into small and degenerate, both types were included as small, even though degeneration had not proceeded very far. Degeneration of eggs seems to occur most usually in ovarioles at the ends of the oviducts.

Some information on the sizes of eggs in small and degenerating ovarioles in *Chrotogonus hemipterus* from Kilosa (Central Line) is presented in Table VI.

TABLE VI.—*Sizes of eggs in mm. in* Chrotogonus hemipterus *dissected 24 hours after capture. " Degenerating " ovarioles are those in which egg 1 is degenerating*

Ovarioles					
Normal		Small		Degenerating	
Egg 1	Egg 2	Egg 1	Egg 2	Egg 1	Egg 2
3·15	1·08	1·35	0·90	1·80	0·90
2·61	0·90	1·80	0·90	.	.
3·60	0·90	.	.	1·80	0·90
3·60	1·35	1·80	0·90	1·80	1·35
4·50	1·35	1·08	0·63	2·70	1·35
4·50	1·35	1·35	0·63	1·80	1·35
2·88	1·26	1·80	0·90	2·25	1·35

It is apparent that where egg 1 has never grown, egg 2 is also smaller than usual, while where egg 1 has degenerated, egg 2 is not smaller than in a normal ovariole. Table VII gives some observations on 60 specimens of *Trilophidia*

TABLE VII.—*Percentages of small and degenerating ovarioles in specimens of* Trilophidia conturbata *kept for various periods without food*

Period kept	12 hours		36 hours		60 hours		84 hours	
Number dissected	10		10		17		23	
	Small (%)	Degen. (%)	Small (%)	Degen. (%)	Small (%)	Degen. (%)	Small (%)	Degen. (%)
	6·7	1·3	3·9	6·6	6·4	11·1	12·6	9·4

conturbata confined singly for varying periods without food. The percentage small ovarioles does not rise until after 60 hours, while the percentage degenerating ovarioles increases up to this time, then falls, presumably because, degeneration of egg 1 being then complete, ovarioles which had been degenerating were classed as small. These observations tend to confirm that degeneration of egg 1 is connected with shortage of food.

Roonwal (1946) suggested that reabsorption of small ovarioles in fourth-stage hoppers of *Schistocerca gregaria* leads to asymmetry. Some of my observations on *L. m. migratorioides* (Phipps, 1950) also suggested that reabsorption of ovarioles in old adults might lead to an increase in asymmetry. However, from Table I, there is no relation between percentage small ovarioles and total ovarioles, while asymmetry has been shown to be related to ovariole number. The evidence therefore shows that there is no connection between asymmetry and small ovarioles but that, just as variability increases with rise in number of ovarioles, so also does asymmetry. This seems compatible with Dancoff's Principle of Maximum Error (Quastler, 1953).

Rudiment Number

The average number of egg rudiments per ovariole in each stage is shown for some species in Table VIII. The number of individuals used in computing the means for the species dissected through a year is the number of each stage recorded in Table V. For the other species, the number of individuals is given in brackets. This information is included because it has not been recorded before for many of the species; the work of Richards and Waloff (1954) has tended to confirm my observation (Phipps, 1949) that new rudiments may be produced during the life of a grasshopper. The figures in Table VIII indicate that this also occurs in East African grasshoppers, as in most species the average number of rudiments is lower in stage I than in later stages and reaches a maximum in stage II or III.

V. HABITATS AND SEASONAL OCCURRENCES

The following account summarises general observations on the occurrence of the species dissected throughout a year, based on notes made during searching as described in Section III. Remarks on the occurrence of nymphs are based on casual observation of these in the course of collection. In each period some of the species being dissected were those which occur mainly on bare ground or short grass and others those which occur mainly in thick herbage, so that at no time was only one type of habitat being searched regularly. The occurrence of a high proportion of specimens with eggs in the oviducts and of specimens in

TABLE VIII.—*Average numbers of egg-rudiments per ovariole in successive ovarian stages for certain species*

Species	Stages I	II	III	IV
P. pedestre	13·7	15·1	15·7	15·0
Parepistaurus sp. n.	17·4	19·1	21·3	20·2
P. lobicercus	19·4	.	23·3	20·6
P. tectifera	10·0 (1)	.	13·3 (2)	14·8 (10)
I. burtti	13·5 (1)	17·3 (3)	16·9 (3)	16·0 (6)
E. ornata	9·6 (3)	10·7 (2)	11·5 (2)	12·4 (1)
C. melanostictus (Mlingano)	14·2	18·0	17·1	17·3
C. melanostictus (Morogoro)	9·0	.	14·0	16·0
P. decoratus	11·0	11·8	15·1	13·7
S. gregaria	15·4 (6)	.	.	.
O. poultoni	11·7	11·6	13·4	13·0
C. glaucopsis	12·1 (7)	11·6 (1)	11·6 (2)	12·1 (11)
Aiolopus sp.	15·1	23·4	20·2	18·4
M. fasciata	15·8	19·2	18·2	18·4
T. conturbata (Mlingano)	15·6	19·0	19·3	18·2
T. conturbata (Morogoro)	13·8	18·0	16·5	15·4
G. temporalis (Mlingano)	18·7	28·2	23·8	21·4
G. temporalis (Morogoro)	18·4	24·2	18·0	21·3
C. hemipterus (Mlingano)	11·6	10·9	13·1	13·0
C. hemipterus (Morogoro)	11·5	10·5	12·5	12·4
P. olivaceus	6·8 (2)	.	9·4 (1)	9·4 (6)
Z. elegans	.	7·4 (4)	6·2 (11)	5·1 (9)
Lamarckiana sp.	8·8 (1)	.	12·4 (5)	13·0 (4)
P. hippiscus	6·2 (2)	7·4 (1)	7·5 (3)	7·0 (3)
Thericles gnu	10·0 (1)	.	11·4 (1)	10·1 (5)

stages I and II is interpreted as indicating periods, usually short, in which outbursts of oviposition or adult emergence respectively were going on. These periods are summarised in Table IX. For some species mention is made in the text of considerably longer periods during which there was evidence of some oviposition or adult emergence. These are based on smaller numbers with eggs in the oviducts, or in stages I or II.

The general summary for each species cannot at present be applied anywhere outside the area actually searched, as casual observations in other places only 10 or 20 miles away often showed the presence of species which had been sought in vain in the usual catching areas.

Sub-family CATANTOPINAE

Parepistaurus sp.

This species occurs mainly in long grass and thick herbage. One place at Mlingano where specimens could usually be found was a clump of elephant grass, another a thick hedge. It seems to be restricted to these habitats. It prefers to rest on plants and often creeps into grass when disturbed. Though it is micropterous, this habit makes it less easy to catch than might be expected.

It occurs as an adult throughout the year, being less numerous in June and July. During and after this period nymphs are present giving rise to new adults from August onwards. Oviposition begins in October and continues into the

next year, but some adult emergence and oviposition goes on during every month.

Catantops melanostictus Schaum

This species is normally found in thick growths of grass and herbaceous plants. At Mlingano it was caught chiefly in an area covered with grasses, *Asystasia gangetica*, *Commelina benghalensis* and small bushes. When very abundant it spreads into short grass and may even be taken by hand. Such a

TABLE IX.—*Periods of outburst of oviposition and adult emergence*

Species	Oviposition periods	Total stage IV dissected	Number with eggs in oviducts	Adult emergence periods	Total dissected	Total stages I and II
Parepistaurus sp. n.	11.x.52	5	4	6.ix–5.x.52	24	13
	29–30.xii.52	4	4	29–30.xii.52	10	6
	17.i–1.ii.53	15	8	.	.	.
C. melanostictus	7–13.viii.51	5	3	1.vi–19.vii.52	30	27
	2.ix.51	4	2	.	.	.
	1–22.iii.52	13	6	.	.	.
	19–26.vii.52	4	4	.	.	.
	x.52	17	7	.	.	.
P. decoratus	viii.52	16	6	24.xii.52–	31	25
	25.ii.53	5	3	10.i.53	.	.
O. poultoni	8–27.xi.52	9	6	14.ix–25.x.52	35	19
	16–22.iii.53	13	6	1–24.ii.53	12	5
				21–30.viii.53	20	10
P. pedestre	22.xi.52	5	4	19–25.x.52	7	6
	18–19.iv.53	11	10	26.i–22.ii.53	15	13
Aiolopus sp.	18–23.ix.51	3	2	29.ix.51	6	6
	13.x.51	6	5	1–13.vii.52	12	12
	16.xii.51–27.i.52	25	18	.	.	.
	1–23.iii.52	14	6	.	.	.
	8–21.vi.52	9	5	.	.	.
M. fasciata	6–13.i.52	7	4	5–6.vii.52	10	7
	13–19.iv.52	7	5	.	.	.
	24.v–8.vi.52	11	7	.	.	.
A. patruelis	10–17.i.53	8	6	20–27.xii.52	10	7
	24.ii.53	5	4	.	.	.
	24–31.v.53	6	5	.	.	.
T. conturbata	14.xii.52	5	3	2–9.viii.52	10	5
	2–16.i.53	9	6	1–8.ii.53	9	6
	15–17.iii.53	10	4	.	.	.
	14–28.vi.53	8	5	.	.	.
G. temporalis flexuosus	20.x.51	5	4	None	.	.
	9–24.xii.51	5	4	.	.	.
	vi.52	14	8	.	.	.
C. hemipterus	13.i–19.iv.52	57	38	4–10.v.52	10	7
	1.vi–26.vii.52	21	19	2–3.viii.52	5	3
	8.xi–20.xii.52	21	20	19–25.x.52	10	6

spread occurred in August 1950 at Muheza Hospital and in March–August 1953 at Mlingano. It is shy and difficult to catch when not abundant. After a flight it usually comes to rest on a vertical stem, head up, and on the opposite side of the stem from its pursuer. It then often backs down the stem and may drop to the ground where it is concealed amongst the undergrowth. Here it usually remains quite still and if seen can be taken by hand.

The nymph is green and newly-emerged adults are the same colour with the adult pattern very faintly marked. This pattern is fully-developed within a few hours. Nymphs have been seen feeding on *Geranium* at Morogoro.

The species occurs throughout the year and there is no regular annual period of scarcity, since during September–December 1951 it was scarce but during the same period of 1952 abundant at Mlingano. The incidence of Stage I in dissections suggests that emergence of new adults occurred during June and July 1952; the occurrence of adults with large fat bodies in January–April 1952 suggests emergence of new adults in this period. There is thus evidence of adult emergence in all months except September–December. Oviposition appears to occur mainly between March and October. Nymphs were especially numerous in April–May and November 1952 and in March 1953.

Phaeocatantops decoratus (Gerstaecker)

This species occurs, like *C. melanostictus*, amongst fairly thick herbage, and behaves very similarly to it when pursued. It does not, however, spread into short grass when numerous. It occurs throughout the year but is rather less abundant from September to November. Nymphs are especially numerous from March to November.

Oxyaeida poultoni Ramme

This occurs in thick herbage with heavier bush growth than that favoured by the last two species, but spreads into lighter vegetation when abundant. Where long grass has been cut and piled on the ground it sits on this and tends to burrow into it, as also into thick tall grass. Because of this habit it may be difficult to catch even when fairly abundant.

It appears to have a fairly definite seasonal occurrence. Adults are numerous from September to May but uncommon from June to August. The occurrence of nymphs in July and August supports the conclusion from dissections that an adult emergence period occurs from late August to October, presumably arising from eggs laid in March. Similarly, the eggs laid in November 1952 may have given rise to the adults which emerged in February 1953.

Paraspathosternum pedestre Miller

This species is found mainly in long grass to which it appears to be restricted. It is phytophilous but less inclined to burrow into vegetation than *Oxyaeida poultoni* and is not difficult to catch. It shows a fairly definite seasonal periodicity, adults being especially abundant from September to November, less abundant in December, more abundant following a new adult emergence in January–February, and continuing abundant until May. Presumably the adult emergence in October followed oviposition in April and that of January–February the

oviposition period in November. The presence of nymphs in July–September would agree well with the April oviposition period.

Sub-family Acridinae

Aiolopus sp.

This species occurs amongst grass, short or long. Quite small " islands " of grass, *e.g.* at a cross road, may be populated and the grasshoppers may also sit on the path in the neighbourhood of such patches, but they are mainly phytophilous. Even when numerous this species does not spread far into thick herbage. It is fairly easy to catch as its usual habitat does not afford hiding places, but it is capable of quite long flights. It occurs throughout the year, but it is possible to distinguish two imperfectly separated generations on the score of adult emergence and of death of the old population in June and December, in which months large numbers were found hanging on grass stalks in the attitude typical of grasshoppers which have died of " fungus ". These deaths were followed by short periods of scarcity. In Morogoro the species was abundant during February and March 1955, when all of 10 specimens dissected were in stage IV.

Morphacris fasciata (Thunberg)

This species is geophilous and was usually found sitting on paths or bare earth. The nymphs are like the adult and occur amongst grass and herbage. Adults are also not infrequently found in herbage bordering a path. Adults occur throughout the year, but tend to be scarce in September–October and February–March. Oviposition and adult emergence periods indicated by dissections do not link up very well, but it is likely that nymphs seen in April gave rise to the adults of May, June and July.

Acrotylus patruelis (Herrich-Schaeffer)

This species, like *M. fasciata*, is geophilous and sits on paths and bare earth, but it may be found especially after rain in grass borders, etc. It has also been seen frequently on sand. There is a fairly clear indication of seasonal occurrence. It is fairly abundant in December–February and again in May and June. Oviposition occurs in both these periods and new adults appearing in December may arise from eggs laid in May and June, though this would appear to necessitate a diapause. However, the occurrence of at least one or two in every month except September, and the fact that all stages were represented in every month except November when only stage IV was found, indicates that some adult emergence probably goes on throughout the year.

Trilophidia conturbata (Walker)

This species is also geophilous and is found mostly on paths and bare earth, or under bushes bordering them. When abundant it may also spread into short grass. It has also been found amongst fairly thick vegetation after rain, an observation which has also been made on *M. fasciata* and *A. patruelis*. Nymphs of these species are found amongst vegetation and do not sit on bare earth as do adults. This suggests that young adults may tend to remain in the nymphal

habitat for at least some days after emergence. It was also noted that *T. conturbata* yields few stage I in dissections. This would tend to support the suggestion made here and to lead to the conclusion that, though these species are more obvious on bare earth, the true "home", where oviposition and nymphal development occur, is amongst vegetation. Near Morogoro, at Magado, these grasshoppers were found in August, 1954 in Sudan grass which formed a thick though low mass of vegetation. They were said to eat the leaves of some varieties of roses. Sixty females were taken in the course of about one hour. This species occurs all the year round with some indication of main adult emergence periods in August and February and oviposition in December–January and March–June.

Gymnobothrus temporalis flexuosus (Schult.)

This species is normally common in cultivated areas, edges of gardens, etc. It usually sits on the ground. When very abundant it may also be found in long and short grass and even in thick herbage. It appears to be present throughout the year, adults becoming slightly less numerous in November and December.

In Morogoro it was abundant during May–July 1954, then uncommon until January, 1955. In February 1955, 5 out of 7 dissected, all stage IV, had eggs in the oviducts.

Family Pyrgomorphidae

Chrotogonus hemipterus Schaum

This species is geophilous and is found especially on cultivated ground or at least soft soil, not on hard-beaten paths. It spreads into short grass when very numerous. It is also often found on sand beside rivers, dry or flowing, and on sandy roadsides. It has been seen to feed on radish leaves. It occurs throughout the year, but there is evidence that separate colonies, even within a short distance of each other, may have different periodicities. Three or four colonies were recognised at Mlingano, one to the north of a valley about half-a-mile wide (northern), separated by this valley from a south-western and a south-eastern colony, about a quarter of a mile from each other. The south-western colony could also be divided into two parts, the main colony and a smaller colony to the north of it and about a quarter of a mile away. Adults in the main south-western colony were abundant in January, February and early March and the second half of May. Oviposition occurred here from January to April and adult emergence in early May. They were scarce from July to September, after which no more observations were made. The northern colony was observed from late March to December and adults became abundant only during June–December, oviposition occurring in June–July and November–December, and adult emergence during early August and mid–October.

In March, 1952, in the smaller part of the south-western colony, only macropterous forms were seen ; in the main south-western colony both macropterous and brachypterous forms and in the south-eastern colony only brachypterous forms.

The existence of separate colonies in this species is not surprising, as even macropterous forms fly weakly and for short distances. It is, however, remarkable that in adjacent areas where meteorological conditions are the same and

no very great differences in soil and vegetation exist there should be two different periodicities. It is difficult to escape the conclusion that genetic differences must exist between separate colonies. This conclusion is also supported by the differences in the proportions of macropterous and brachypterous forms noted above.

In the Morogoro area *C. hemipterus* was fairly abundant from May, 1954 to February, 1955, but this includes collections at points between Ruvu and Kilosa, a distance of about 170 miles, and must have covered many colonies.

It is apparent from Table X that there is great difficulty in separating the year into wet and dry periods, as there was some rain in every month and at least five days with measurable rain in almost every month. Quite frequently, in the midst of a dry spell lasting two weeks or more, there were one or more

TABLE X.—*Monthly rainfall in inches at Mlingano*, 1951–53

1951	Rainfall	Days with measurable rain	1952	Rainfall	Days with measurabl rain
August	1·55	13	August	0·94	14
September	0·74	10	September	3·49	14
October	9·88	17	October	4·48	11
November	14·24	21	November	6·01	19
December	7·87	16	December	0·10	2
1952			1953		
January	0·20	4	January	1·90	9
February	2·27	3	February	1·03	2
March	2·06	5	March	3·04	13
April	2·27	7	April	7·20	21
May	6·11	15	May	11·37	25
June	1·79	14	June	0·78	3
July	0·27	9	July	1·92	11

days of heavy rain, up to half an inch, and it is very difficult to estimate the effect of this on grasshoppers. It was attempted to relate amounts of rainfall and numbers of wet days to the number of ovarioles per individual, the percentage small ovarioles and the number of rudiments per ovariole, but without success except in *Catantops melanostictus*, where the linear regression of percentage small ovarioles on rainfall, both by months, was significant (*b* positive). This result is not regarded as reliable, however, in view of the lack of any relation in other species. The absence of such a relation is not altogether surprising, as the condition of the ovaries may be expected to be influenced by the past weather, and it is scarcely likely to be profitable to look for evidences of such influence until the duration of the nymphal stages and of the maturation stages are more precisely known. There is no obvious relation between outbursts of oviposition or adult emergence and rainfall or soil temperature (of which daily records were kept) for any species.

A periodicity is noted, however, in the average number of eggs in the oviducts for some species. Comparisons of mean egg numbers in the oviducts in wet periods (with an average of more than 0·04 inch rain per day, and with rain on more than half the days) and dry periods (with an average of less than 0·04 inch rain per day and with rain on only a few days) were made for *Gymnobothrus*

temporalis, *Aiolopus* sp., *Morphacris fasciata*, *Oxyaeida poultoni*, *Parepistaurus* sp. n. and *Paraspathosternum pedestre*. For the other species the means differed only slightly. Of those tested, the difference was significant only for *Aiolopus* sp., with an average of 27·0 eggs per female in wet periods and 22·0 in dry, ($P < 0{\cdot}01$). It was also noted that in some species there appeared to be periods, not correlated with rainfall, during which the mean number of eggs in the oviducts was low. This was also tested, separation of the periods being made by inspection of a chronological list of egg numbers, with the following results :

Species	Periods	Mean numbers of eggs	Significance of difference
C. hemipterus	Aug., 1952–Dec., 1953	25·86	$P < 0{\cdot}001$
	Jan., 1953–July, 1953	19·1	
M. fasciata	1st Aug., 1951–30th Apr., 1952	31·06	$P < 0{\cdot}001$
	1st May, 1952–31st July, 1952	21·73	
Aiolopus sp.	1st Aug., 1951–6th Jan., 1952	28·1	$P < 0{\cdot}001$
	13th Jan., 1952–31st July, 1952	21·7	
Parepistaurus sp. n.	1st Aug., 1952– 17th Jan., 1953	7.13	$P < 0{\cdot}001$
	24th Jan., 1953–31st July, 1953	6·00	

For the other species, there were no obvious periods with fewer eggs. It is interesting that for these four species there is a period from August to January (April in *M. fasciata*), covering the short rains, during which a female produces on the average more eggs per pod than in the rest of the year, which includes the long rains. The fact that this difference was found both in 1951–52, when the short rains of 1951 were exceptionally heavy and the long rains of 1952 light, and in 1952–53, which was a much more normal year as regards distribution of rainfall, suggests that there is a seasonal periodicity for some species which is not necessarily related to weather. The state of affairs in *C. hemipterus* may also be related to areas searched, and this is accordingly discussed further in the next section.

Zonocerus elegans alone among East African grasshoppers dealt with in the present study appears to have a definite seasonal cycle. It was not found in the Muheza–Mlingano area, but a few were caught near Korogwe, about 60 miles from Tanga, in January 1952. It is a well-known seasonal pest on the Central Line, where adults may be found from October to February, after which they disappear. Nymphs are not usually obvious before September. This species is the only one considered in which it appears necessary to postulate the occurrence of a diapause, presumably in the egg. The general observation that there were periods in which it was difficult to find grasshoppers in Morogoro, however, suggests that other species may enter diapause in that area.

VI. Geographical Differences

It has been mentioned above that differences in the mean number of eggs in the oviducts may exist between populations of *C. hemipterus* from different areas. The colonies, all at Mlingano, have been mentioned in section V. The mean number of eggs per female in the northern colony in August–December

1952 was 25·86, in the southern colonies in January–March 1953 it was 19·75 and in all areas in April–July 1953 it was 18·41. The mean for the northern colony is significantly greater than that for the southern colonies, and it is uncertain whether this is due to the seasonal effect described above or to differences between the populations. The former appears most likely, as the mean for all areas is lower, though not significantly so, than that for the southern colonies. If there is a difference between grasshoppers from the northern colony and those from the others, this would support the suggestion made above as to the existence of genetic differences between the populations.

TABLE XI.—*Comparisons between grasshoppers from the Tanga area* (*T.A.*) *and Central Line Area* (*C.L.A.*), *in respect of ovarian development*

Species	Mean ovariole number		Average eggs in oviduct		Mean length of egg in mm.		Numbers dissected	
	T.A.	C.L.A.	T.A.	C.L.A.	T.A.	C.L.A.	T.A.	C.L.A.
O. luridus	52·0	63·3	.	.	.	.	7	3
E. exigua	8·8	7·9	7·7	.	4·20	.	6	4
P. lobicercus and *Parepistaurus* sp. n.	8·0	8·0	6·7	7·3	4·33	4·20	186	15
A. subnuda	19·0	23·6	19·0	24·0	6·12	5·12	1	5
C. melanostictus	29·1	33·4	27·6	34·0	4·71	4·05	170	7
P. decoratus	34·6	35·6	28·9	.	4·99	.	224	4
T. caerulescens	136·3	122·0	82·0	.	.	.	7	9
C. oberthuri	121·9	109·0	.	.	.	.	9	5
C. speciosa	50·3	60·0	.	.	.	.	3	2
Aiolopus sp.	30·8	32·1	25·0	30·0	3·86	3·89	202	10
A. longicornis	37·4	37·6	30·5	34·0	.	4·40	10	11
M. fasciata	35·2	36·0	28·0	35·0	4·77	4·14	178	6
T. conturbata	23·6	22·1	17·1	19·2	3·71	3·69	209	35
A. patruelis	23·1	24·6	16·9	.	3·94	.	87	8
O. citrinus	35·0	36·8	.	38·0	.	4·68	2	5
H. tenuicornis	47·2	47·3	41·5	.	.	.	19	6
G. africanus	72·4	119·0	.	.	.	.	10	1
P. tricolor	159·3	130·5	116·0	.	.	.	10	3
G. temporalis	16·3	16·2	12·7	16·7	4·06	4·10	208	18
O. brachypterus	16·5	16·2	.	.	.	.	2	9
P. squalus	26·7	27·0	25·0	23·8	4·25	4·60	3	13
C. hemipterus	27·7	29·6	21·0	22·2	4·44	4·46	237	76
T. calliparea	99·4	96·0	.	.	.	.	10	3
Z. elegans	108·0	127·0	121·0	.	6·25	.	6	21

Figures for comparison between the Tanga and Central Line areas are set out in Table XI. Few examples of many species from the Central Line were dissected and tests of significance of differences were made only for ovariole numbers in *C. melanostictus*, *T. caerulescens*, *C. oberthuri*, *O. luridus*, *C. hemipterus*, *Z. elegans*, *G. africanus*, *Aiolopus* sp., *A. subnuda* and *P. tricolor*; and for numbers of eggs in the oviducts for *Parepistaurus*, *C. hemipterus*, *M. fasciata*, *G. temporalis*, *Aiolopus* sp., *A. longicornis* and *T. conturbata*. The differences were significant for ovariole number in *O. luridus* ($P < 0{\cdot}001$), *A. subnuda* ($P < 0{\cdot}05$), *G. africanus* ($P < 0{\cdot}001$) and *P. tricolor* ($P < 0{\cdot}001$); and for numbers of eggs in *G. temporalis* and *Aiolopus* sp. (both $P < 0{\cdot}001$).

In all these, except *P. tricolor*, the specimens from the Central Line appear to produce more eggs than do those from the Tanga area. This tendency is suggested, too, in some of the other species, for which too few observations were available to make significance tests worth while. In some species the average length of the egg is less on the Central Line than in the Tanga area. The differences were significant for *C. melanostictus* ($P < 0{\cdot}001$) and for *M. fasciata* ($P < 0{\cdot}02$), but not for *T. conturbata* and *Aiolopus* sp., the only other two species tested. The eggs are thus smaller in Central Line specimens in two species in which neither the ovariole number nor the number of eggs in the oviduct is greater. It is, however, possible that examination of more specimens might show that these differences occur in other species—that more but slightly smaller eggs are produced by grasshoppers from the Central Line than by those from the Tanga area.

Macropterous and brachypterous forms of *C. hemipterus* were compared as to number of ovarioles and mean number of eggs, but no significant differences were found.

VII. Abnormalities

A number of abnormalities were noted in the ovaries, most of them being similar to those I have described in British grasshoppers (Phipps, 1949). Some of these are illustrated in figure 1. They are largely related to failure to ovulate in one or more ovarioles.

An interesting abnormality for which it is difficult to account is that illustrated in figure 1*b* (*C. hemipterus*), in which egg 1 was double in one ovariole and egg 2 double in a neighbouring one of the same ovary, the others being normal. The doubling of egg 1 might have been produced by a delay in ovulation of the egg below it, and the same thing appears to be happening in the ovariole in which egg 2 is double. The egg development in these ovarioles appears to be out of step.

One specimen of *C. melanostictus* was found in which each oviduct contained 28 eggs, the ovariole number being the normal 14 + 14. Obviously this individual had failed to oviposit before ovulating again. The ovary was otherwise normal.

VIII. Discussion

It is unfortunate that it was not possible to check the duration of the ovarian stages in any species, but more recent work in Sierra Leone (Phipps, 1959), indicates that in *Paracomacris centralis centralis* (Rehn) the interval between final ecdysis and first oviposition is about 14 days, and the inter-pod period 4–5 days. If this is approximately true of the small East African grasshoppers, as it may well be, from Table V the average length of female adult life is 4–5 weeks, during which 3–4 egg-pods would be laid.

In the discussion of habitats and seasonal occurrence which follows, " the Sudan " refers to the observations of Joyce (1952) and " the Rukwa " to those of Chapman and Robertson (1958). In general, grasshoppers are found in relatively drier situations in Tanganyika than in the Sudan. Thus, *C. axillaris*, reported by Joyce from moist soils, was found on the coast at Pangani, in vegetation just above the sand beach ; in fact the grasshoppers often flew on to the beach. In the Rukwa it occurs on grassy plains. *P. tricolor* and *C. melanostictus*

in the Sudan are typical of swamps; in Tanganyika the former is found near streams or pools, in long grass and the latter in dense vegetation on moist soils. *O. hyla* and *Jasomenia* sp. are typical in the Sudan of bare wet ground; in Tanganyika the former occurs amongst thick vegetation in damp places and the latter (not necessarily the same species as that studied by Joyce) near water, also in vegetation. *M. fasciata* in the Sudan occurs on wet soils, and Kevan

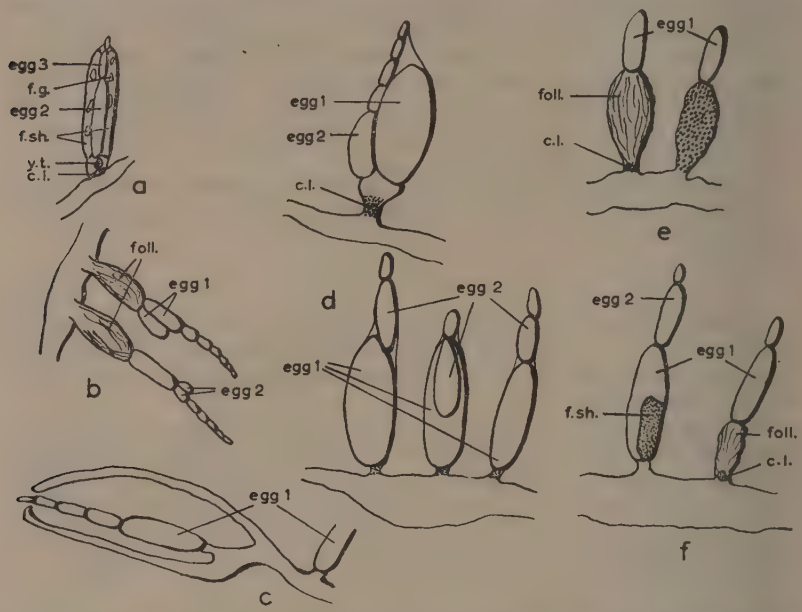

FIG. 1.—Abnormalities. (*a*) One ovariole of *C. melanostictus* showing degenerate egg 1 surrounding eggs 2 and 3; (*b*) two ovarioles of *C. hemipterus* showing egg 1 double in one and egg 2 double in the other; (*c*) anterior end of ovary of *P. decoratus* showing duplication of accessory gland; (*d*) one ovariole from one ovary and three from the other of *Parepistaurus* sp. n. showing egg 2 pushing down beside fully-formed egg 1; (*e*) two ovarioles of *T. conturbata* showing one normal empty follicle and one filled with a mass of degenerating egg; (*f*) two ovarioles of *P. pedestre* showing one normal empty follicle and one in which ovulation has not occurred. *c.l.*, corpus luteum; *f.g.*, fat globules; *foll.*, empty follicle; *f.sh.*, flattened shell of egg; *y.t.*, mass of yellow tissue.

(1950) has noted it chiefly on mud in Kenya. In the Tanga area it can always be most easily found by walking over bare ground and paths, and though it may fly into vegetation when disturbed, it returns later to the bare area. In the Rukwa it is found in open scrub. It has been mentioned that nymphs of this and other species occur on moist or wet soils (Joyce's classification) in Tanganyika, and there may well be a change of habitat in the adult.

Humbe tenuicornis and *Oedaleus senegalensis*, noted by Joyce as occurring on dry soils, form an exception to the generalisation made above, as they were found mainly on moist soils in the Tanga area, though *H. tenuicornis* could

usually be found on hill slopes with rock outcrops near Morogoro. In the Rukwa it is found in open scrub.

Rainy seasons in the Sudan (June–October) and the Rukwa (November–April) are sharply defined, and many grasshoppers which breed throughout the year in the Tanga area have a well-marked seasonal distribution in the Sudan and the Rukwa. In the Sudan most species oviposit during 4–8 weeks, mostly in June and July ; in the Tanga area oviposition goes on throughout the year, while in the Rukwa most species again oviposit during the rains and many enter diapause as egg or adult during the dry season. *Acrotylus patruelis* survive the dry season in the Sudan as inactive adults in cracks and it is possible that in the Tanga area this species also hides in such places for short periods, which would account for its intermittent scarcity. *M. fasciata* and *C. melanostictus*, which survive the dry season in the Sudan as active adults largely confined to damp valleys, breed continuously in the Tanga area, though with periods of scarcity. In the Rukwa, eggs of *fasciata* can be found during most of the year, those of *melanostictus* only during the rains. A few grasshoppers breed continuously in all areas whatever the rainfall distribution. In the Sudan these include *Trilophidia* sp., *Chrotogonus* sp. and *Aiolopus* sp. (near *thalassinus*). These may not be the same as the species studied in Tanganyika, but it is the Tanganyika species of these genera which show least tendency to periods of scarcity. In the Rukwa, *C. hemipterus* breeds throughout the year and *Aiolopus thalassinus* has two broods in the year, as was indicated also in the Tanga area. It is therefore clear that different species vary in their dependence on rainfall, and this presumably reflects differences in their adaptations. It is possible that some of the species considered in the three regions occur in different habitats but with the same microclimate, as suggested by Bei-Bienko (1930).

The observations on ovariole numbers may also be compared with those of Waloff (1954) and on egg numbers and sizes with those of Chapman and Robertson (1958), both for specimens from the Rukwa. There may be significant differences in ovariole numbers in some species. Rukwa specimens have more ovarioles than those from the areas I have considered in *P. squalus*, *M. laticornis*, *H. thoracica*, *Chrotogonus* sp. and *C. melanostictus*, but fewer in *M. fasciata*, *Gastrimargus* sp. and *A. viridipennis*. Nolte (1939) found 14 + 14 ovarioles in *Acrotylus patruelis* from the Transvaal, while Waloff (1954) found 7 + 7 in one from Khartoum. My specimens had numbers nearer to 14 + 14, both from the Tanga and Central Line areas, except two at Mlingano which had 8 + 9 and 7 + 8, and one from Kilosa which had 8 + 8.

My specimens of *S. gregaria*, all pink, with ovaries in stage I, had fewer ovarioles than those quoted by Waloff (1954) but more than the numbers of eggs per pod given for cage-bred specimens by Norris (1952). I am indebted to Mr. P. R. Stephenson of the Desert Locust Survey for the information that my specimens, taken near Handeni in February 1954, probably originated from the Somali Peninsula and became adult in late December, 1953 and early January, 1954. They were thus one month old, but showed no development of the ovaries.

Chapman and Robertson described the egg-pods of a number of species. They point out that egg-length varies greatly, according to the amount of water imbibed from the soil, so it may be appropriate to compare their minimum egg-lengths with mine. In all species where a comparison is possible, except

Aiolopus thalassinus, their minimum egg-lengths are less, which lends some support to the view that there is a geographical variation in some species. My results also indicate that Central Line specimens of *Aiolopus* sp. do not lay smaller eggs than those from the Tanga area. It is unfortunately not possible to compare mean egg numbers, as Chapman and Robertson (1958) give only maximum and minimum numbers. These agree in the main with my numbers from the oviducts ; in only a few cases is there any indication that maximum egg number in the Rukwa is greater than in the Tanga area. One pod of *C. melanostictus* from the Rukwa contained 74 eggs, and it is most unlikely that these were the result of one ovulation. It is possible that retention of the eggs in the oviducts, indicated by my abnormal specimen, may be not unusual in this species.

The status of grasshoppers as pests in Tanganyika is difficult to define. Most of the agriculture is of a shifting type carried on by Africans who take little note of the pests of their crops. Sisal, the only crop grown on a large scale by Europeans, does not appear to be attacked by Acrididae. The only reliable evidence bearing on this point comes from European gardeners, and this is, of course, small scale damage, though the whole garden may be stripped in some areas by *Zonocerus elegans*. Of the other species, it is possible that *C. hemipterus* might become a pest, especially as it breeds continuously, apparently throughout its range. It is especially abundant on newly-turned and therefore partly bare soil and was responsible for the destruction of seedling radishes at Mlingano on several occasions. *G. temporalis* is very much a grasshopper of cultivation and the bush immediately surrounding it. Its food is not known, but it might become destructive, at least in gardens.

IX. Summary

The results are recorded of dissections of 6 species of Lentulidae, 8 of Pyrgomorphidae, 1 of Pamphagidae, 6 of Eumastacidae and 90 of Acrididae (including 34 Catantopinae, 4 Calliptaminae, 4 Hemiacridinae, 40 Acridinae and 8 Truxalinae). Most of the work was done within 30 miles of Tanga, but some observations were made in the neighbourhood of Morogoro. The number of ovarioles and their relation to female length and the average number of eggs in the oviducts are recorded for each species.

The regressions of ovariole number on female length are significant for Pyrgomorphidae, Catantopinae, Acridinae and Hemiacridinae, and also for some of the groups into which the three Acridid subfamilies are divided. The average number of ovarioles per millimetre length of female is rather low for many Acridinae and Catantopinae, and is much greater in Pyrgomorphidae.

Asymmetry between the two ovaries in ovariole number increases with increase in the number of ovarioles. It is unlikely that asymmetry is caused by reabsorption of ovarioles during adult life.

The sizes of egg 1 in the four stages into which development of the ovaries is separated are recorded. It appears that the size of this egg at the final moult, and its size when yolk begins to be laid down in it, are not closely related to the size of the grasshopper. Though large species lay larger eggs than small species, the linear regression of egg-length on female length being significant, the eggs laid by small species are not proportionately smaller than those laid by large

ones, and it is suggested that small grasshoppers have fewer ovarioles because of the necessity of keeping the eggs above a certain size.

The recognition of stage IV by the presence of *corpora lutea* is discussed, and it is considered that this criterion, if used with care, is reasonably reliable. Data are presented showing that in two species lack of food leads to the degeneration of the eggs.

The average number of egg rudiments per ovariole is presented, though it is not regarded as very significant and there is evidence that new rudiments are produced during adult life.

An account is given of habitat and seasonal occurrence in eleven species. All of them were active and apparently reproduce throughout the year, though there were indications of periods of emergence and of oviposition. Some species, which as mature adults were found in dry situations, appeared to favour moister surroundings in the nymphal and young adult stages. It is difficult to find any evidence of the effect of weather on grasshoppers, and in some species there appears to be an annual cycle which is not obviously related to rainfall or temperature.

Comparisons are made for some species between specimens from the Tanga and Morogoro areas, and with observations of other authors in the Sudan and the Rukwa valley. Many appear to produce more eggs in the Morogoro area than in the Tanga area, and in some species the eggs are smaller. For many species, periods of abundance and of oviposition are more clearly defined in the Sudan and in the Rukwa valley than in the Tanga area, but a few oviposit throughout the year in all parts of the range considered.

The status of some of the species as possible pests is discussed, and it is concluded that of those studied only *Zonocerus elegans* (Thunberg) is likely to be a serious pest, though other species may do minor damage in some localities.

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